physical measurements and fields which up to the present time have not been covered satisfactorily by other means of investigation.

The writer is greatly indebted to Dr. J. Gordon Wilson, Head of the Department of Otology Northwestern Medical School, with whom this co-operative research has been done and to whom equal credit for the success of the work is due. The writer is also indebted to Professors Millikan and Lunn of the Department of Physics of the University of Chicago for their helpful suggestions and enthusiastic interest during all the stages of development up to the present time.

[1] John P. Minton and J. Gordon Wilson, "Sensitivity of Normal and Defective Ears for Tones of Various Frequencies," *Proc. Inst. of Medicine, Chicago*, 1921.

[2] John P. Minton, "Physical Characteristics of the Ear," in preparation for the *Physical Review.*

NON-DISJUNCTION AND THE CHROMOSOME RELATIONSHIPS OF DROSOPHILA WILLISTONI

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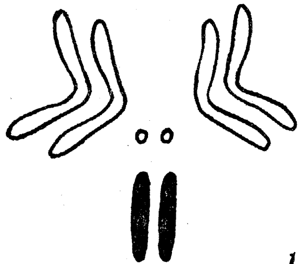
Of the eleven types of chromosome groups found in the genus Drosophila (Metz '16)[7] that designated type A is the most widespread—occurring in 13 of the 29 species that were studied. This type is represented in figure 1. It consists of one pair of rod-like chromosomes, two pairs of long, V-shaped chromosomes and (usually) one pair of very small spherical "m" chromosomes.[1] The constancy of this type among the 13 species is such as to suggest a genetic homology of the respective pairs of chromosomes throughout. On the other hand the species themselves are scattered more or less at random through the genus and do not constitute a restricted taxonomic group. This suggested the desirability of a comparison of the genetic constitution of the chromosomes in two or more of these species.

Since D. melanogaster was already well known genetically and cytologically, and thus afforded a convenient basis of comparison, we undertook a study of D. willistoni,[2] a species resembling melanogaster in appearan e and in chromosome constitution. In the course of this study we have found, by an examination of non-disjunctional flies, that the chromosomal resemblance between willistoni and melanogaster is misleading, for the sex chromosome pair of willistoni does not correspond morphologically to that of melanogaster but corresponds, rather, to one of the autosome pairs of this species. This would indicate that corresponding chromosomes in the two species are not all strictly homologous. The evidence for this conclusion together with a brief discussion is given below.



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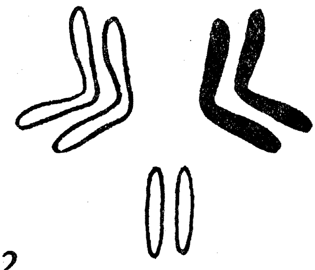

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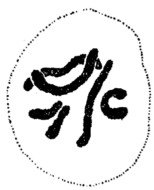

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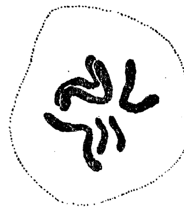

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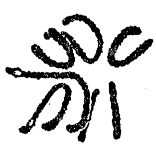

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Figures 1 and 2 are diagrams; figures 3–10 are camera lucida drawings from fixed and sectioned material.[4] Figure 1. Chromosome group of Drosophila melanogaster female; X chromosomes represented in solid black. Figure 2. Chromosomes group of Drosophila willistoni; X chromosomes in solid black. Figures 3 and 4. Normal female groups of willistoni. Figures 5 and 6. Normal male groups of willistoni. Figures 7–10. XXY groups from non-disjunctional females of willistoni.

Cytological Data.—The normal female chromosome group of Drosophila melanogaster is represented diagrammatically in figure 1 and that of D. willistoni in figures 2–4. In melanogaster, as shown by Bridges[6] ('16) in his work on non-disjunction, the rod-like chromosomes are the X chromosomes.[3] These are represented in solid black in the diagrams. In the male of melanogaster this pair is asymmetrical, X being rod-like and Y J-shaped. In the male of willistoni no asymmetry is evident in any pair (figs. 5, 6). Otherwise the chromosomes of willistoni correspond, member for member, with those of melanogaster, except for the possible absence of the minute, spherical pair.

The lack of inequality in the sex chromosomes of the willistoni male necessitated obtaining non-disjunctional flies with three sex chromosomes in order to distinguish sex chromosomes from autosomes. As shown by the genetic data given below these non-disjunctional flies were females having one Y and two X chromosomes. Four chromosome groups from such females are shown in figures 7–10. In each of these there is an extra chromosome, and it is clearly a large and V-shaped one. Since this must be a sex chromosome it proves that the sex chromosome pair in willistoni is one of the long, V-shaped pairs and not the rod-like pair as would have been expected from analogy with melanogaster. We have obtained numerous clear cut figures both of the normal group in each sex and of the non-disjunctional group, and are confident that the evidence is entirely conclusive on this point.

Genetic Data.—In obtaining and identifying the non-disjunctional flies we have followed the procedure used by Bridges ('16) in the case of D. melanogaster. The following summarized account shows the resemblance between the results in the two species and indicates the source of the XXY chromosome groups described above.

Primary non-disjunction appears to be very rare in willistoni and no cases (which could be checked) were observed in our regular experiments. In approximately 150 cultures made especially for this purpose only two cases were detected. In each of these the exceptional fly was a female. The first came from a cross of a rough eyed female by an orange, small-bristle male, both from stock cultures. (Rough, orange, and small-bristle are all inherited as sex-linked recessives.) This mating gave 132 normal daughters, 111 rough eyed sons, and 1 rough eyed (exceptional) daughter (Culture W 1715). Since this rough daughter had already mated with a rough brother, it was not possible to detect "secondary" exceptions produced by her. Six of her rough daughters, however, produced 11 exceptional sons and daughters among 960 significant flies, or 1.14 percent of exceptions. In succeeding generations about the same ration was maintained, as is shown in table 1. For the sake of convenience, this strain has been designated as "line A."

The second primary exception appeared in an entirely unrelated stock, involving the characters two-bristle, short-3, and rough. It gave rise to a second strain known as "line B." Table 1 gives a summary of the breeding tests with this line, which gave results essentially similar to those of line A.

In addition to the ordinary cases of "reductional" non-disjunction we have also detected two cases of "equational" non-disjunction. This type was first described by Bridges ('16) who reported 18 "equational exceptions," i.e., daughters homozygous with respect to a recessive character for which the mother was only heterozygous. In most of his cases, he

was able to demonstrate that crossing over had taken place in one chromosome and not in the other, while in two cases he showed that two crossover chromosomes were present in the exceptional daughter. He explained these facts as due to non-disjunction occurring at the equational division, and believed that they involved crossing over at the "four strand stage" in the primary oocyte.

Of the two certain cases of "equational" non-disjunction in willistoni, one gave a result like that just mentioned. The exceptional fly in this case came from an XXY female (W 1955) which had stubby, orange, small-bristle in one X chromosome, and orange, rough, short in the other. This female was crossed to a two-bristle, short-3 male and produced the following offspring: 135 daughters and 119 sons of the regular classes, 2 two-bristle, short-3 sons (secondary exceptions of the ordinary "reductional" type), and 1 stubby, orange, small-bristle daughter—an "equational" exception. This last female produced secondary exceptions as expected, but she also carried a sex-linked lethal so that her only surviving sons were stubby, orange, small-bristle. Her exceptional daughters, being of the same constitution, also gave this same lethal ratio, but breeding tests from her regular daughters revealed her constitution. By such means it was proved that she had one non-crossover chromosome carrying stubby, orange, and small-bristle, and one crossover chromosome carrying stubby, orange, small-bristle, rough and short, and the new lethal. A non-disjunctional strain was established from this female known as line D (table 1).

TABLE 1

SUMMARY OF BREEDING TESTS

LINE	TOTAL FLIES	EXCEPTIONS	PERCENTAGE OF EXCEPTIONS
A	6671	117	1.8
B	1131	13	1.1
C	701	3	0.4
D	497	22	4.4
Total	9000	155	1.7

The other equational exception is not of special interest since both of her chromosomes were non-crossover chromosomes, as far as the region that could be followed was concerned. It is not certain whether her mother, a descendant of line B, carried a Y chromosome. She gave rise to line C (table 1).

Additional possible cases of equational exceptions have been found but they could not be positively identified as such.

To secure XXY chromosome groups for cytological study the daughter of exceptional females from line A (W 1894b) were used. Theoretically half of these daughters should be of the desired constitution. No attempt

was made to determine whether or not this 1:1 ration was actually realized, but XXY individuals were found without difficulty in the material put up for cytological study.

Discussion.—The evidence is not yet sufficient to indicate the exact relationship between the chromosomes of the two species considered here, but it does indicate that either the chromosomal resemblances are merely superficial or that the sex determining element (gene? or genes?) has been transferred from one chromosome pair to another. A comparison of the sex-linked mutant characters in the two species ought to throw some light on this question. It has not done so up to the present, however, for although we have obtained 27 such characters in willistoni they show so little resemblance to any in melanogaster (either sex-linked or non sex-linked) that they give no clue to chromosomal relationships.

The observed frequency of secondary non-disjunction in willistoni (average 1.7%) was less[5] than that found by Bridges in melanogaster (4.3%). There is no indication at present as to why this should be the case unless the size of the sex chromosomes be considered a factor.

[1] The "m" chromosomes are often difficult to detect. They may be lacking entirely in willistoni.

[2] D. willistoni Sturtevant (D. pallida Williston).

[3] Dr. Bridges kindly informs us that he has subsequently verified this conclusion.

[4] We are indebted to Dr. José Nonidez for making the drawings for figures 3–10.

[5] Line D may possibly be an exception but the small numbers make this doubtful.

[6] Bridges, C. B., *Genetics,* **1,** 1916 (16–52, 107–163).

[7] Metz, C. W., *J. Exp. Zool.,* **21,** 1916 (213–276).

AN APPARATUS FOR DETERMINATION OF THE GASES IN BLOOD AND OTHER SOLUTIONS

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The apparatus consists of a pipette with the upper stem closed by a stopcock, the lower connected with a glass tube. The latter descends 800 mm., then turns at a right angle to connect with a levelling bulb and a mercury manometer open at the upper end. The pipette is calibrated at two points to hold a and A cc., respectively, as shown in the figure.

For an analysis the pipette is filled with mercury. The solution to be analyzed, followed by the reagents to free the gases (e.g., acid for CO_2 in carbonates) is admitted with slight negative pressure through the upper cock, displacing mercury in the pipette. A Toricellian vacuum is created by lowering the levelling bulb, and the meniscus of the mercury in the